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Metabolic adjustments to increasing foraging costs of starlings in a closed economy

Popko Wiersma*, H. Martijn Salomons and Simon Verhulst

Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

*Author for correspondence at present address: Department of Evolution, Ecology and Organismal Biology, Ohio State University, 288 Aronoff Lab, 318 W 12th Avenue, Columbus, OH 43210, USA (e-mail: wiersma.6@osu.edu)

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Summary

Knowledge of the physiological consequences of variation in food availability may be essential for understanding behavioural and life history responses to such variation. To study the physiological consequences of food availability animals are generally subjected to caloric restriction or starvation, thereby reducing the upper limit to the energy budget. The relevance of this approach to free-living animals is questionable, however, because under natural conditions low food availability often results in higher foraging costs, and everything else remaining equal this results in a higher energy budget. We manipulated food availability by varying the foraging costs and studied effects on daily energy expenditure (DEE) and energy allocation of captive starlings *Sturnus vulgaris*. Birds in a closed economy earned their food by flying between two perches 5 m apart. The probability of a reward was set at three different levels, thereby creating a 'poor', 'intermediate' and 'rich' environment. Compared with the rich environment, birds flew 4 times more (2.3 h per day) in the poor environment, and increased DEE by 43% to 220 kJ day⁻¹ (3.7×BMR), within the range of free-living parents rearing young. To our knowledge this is the

first study to show an increase in DEE with decreasing food availability. Body mass, basal metabolic rate (BMR) and pectoral muscle size were reduced in the poor environment. Nocturnal energy expenditure was further reduced by reaching BMR earlier in the night. Calculations show that the energy demands in the poor environment could not be met with the flight costs of 20.5 W that we measured previously in a rich environment. Flight costs derived indirectly from the energy budget were lower, at 17.5 W, probably due to lower body mass. By reducing body mass by 20%, and economising during sleep, the birds achieved savings of 37% in their DEE. Without these savings, a DEE substantially higher than measured in free-living parents rearing young would be required to remain in energy balance. Surprisingly little data exist to verify whether free-living animals use the same tactics to survive periods with low food availability.

Key words: flight cost, BMR, foraging reward rate, *Sturnus vulgaris*, body mass, pectoral muscle size.

Introduction

Fluctuations in food supply are the rule in nature, and animals have evolved numerous adaptations to cope with such fluctuations. Knowledge of physiological or metabolic adjustments to variation in foraging success is essential for making predictions about behavioural choices such as when to leave a site in which food availability decreases, or what levels of energy reserves should be maintained in different environments. The response to diminishing foraging conditions has many dimensions: resting metabolic rate may be altered, mass reduced, and consequently, flight and thermoregulation costs may change (Tiebout, 1991; Deerenberg et al., 1998; Bautista et al., 1998). Therefore daily energy expenditure (DEE), and thus requirements to remain in energy balance, are not simply proportional to the (foraging) activity.

An approach that has frequently been used to study the physiological consequences of food stress is complete or

partial caloric restriction (Daan et al., 1989; Cherel et al., 1994), which by definition results in a decrease in DEE (Fig. 1A). However, when foraging success decreases in the real world, animals that are not sit-and-wait predators have to spend more time and energy foraging for the same amount of food. Everything else remaining equal, DEE is expected to be an accelerating function of foraging costs per reward, because the extra energy spent foraging must also be acquired, which again increases foraging time and energy expenditure, and so on (Fig. 1B). Surprisingly, contrary to this simple prediction, experimental tests found that DEE decreased with increasing foraging costs per reward (Deerenberg et al., 1998; Bautista et al., 1998), thereby superficially resembling the results of caloric restriction experiments. A possible explanation for this counter-intuitive result was suggested by Fotheringham (1998): in his experiments, starlings *Sturnus vulgaris* L. decreased food intake and body mass with decreasing foraging

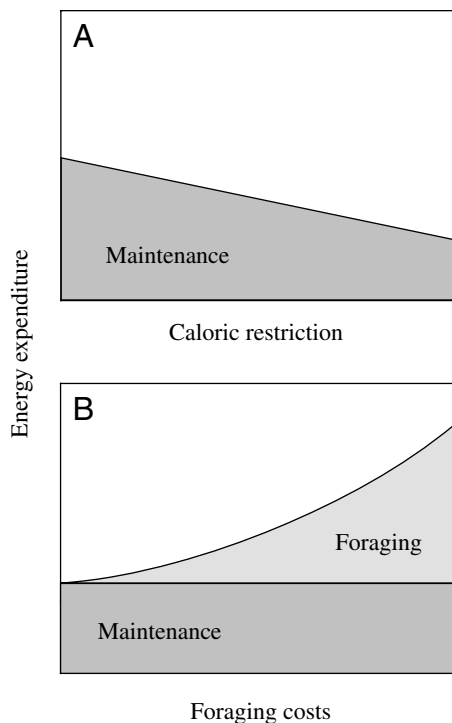


Fig. 1. Daily energy expenditure in relation to food availability manipulations. (A) Caloric restriction results in a decrease in energy expenditure. (B) Increasing foraging costs per reward: when metabolic rate during foraging is higher than when not foraging, and everything else remains constant (mass, nocturnal energy expenditure, etc.), daily energy expenditure is an accelerating function of foraging costs per reward.

reward rate when the number of flights needed for a food pellet was fixed (e.g. 20 flights per reward). But when using variable reward rates (rewarding each flight with a reward with e.g. probability 1/20) they maintained food consumption and body mass (albeit that the range of foraging reward rates was small). Since earlier studies of the relationship between DEE and foraging costs per reward used fixed reward rates (Deerenberg et al., 1998; Bautista et al., 1998), this aspect of the experimental design may explain why they found a decrease in DEE with increasing foraging costs. Fotheringham speculated that cognitive processes, such as motivation or memory, caused the differential response to the variable and fixed reward rates. Whatever the mechanisms, since food reward rates experienced by free-living animals will typically be variable, applying variable foraging reward rates in laboratory studies may prove essential when extrapolating the results to natural conditions.

We studied captive starlings to test the prediction that birds increase DEE with increasing foraging costs. We further quantified the (energy) dimensions over which starlings adapt their physiology to the harshness of their environment (mass changes, time and energy budgets, pectoral muscle size). Following Fotheringham (1998) we rewarded foraging effort with a certain probability that the birds will be given a reward

after a return flight, thereby creating a variable foraging reward rate. We set the foraging costs per reward at three different levels, referred to as a 'rich', 'intermediate' and 'poor' foraging environment.

Materials and methods

Flight cages

Starlings were individually housed in eight indoor flight cages (length×width×height: 5.45 m×0.68 m×0.80 m). Birds earned their food by flying between two perches, 5.00 m apart. Switches on the flight perches were connected to a computer, registering when a bird had landed. The reward (a food pellet) was released into a small tray in front of a feeding perch, which could be reached by hopping 20 cm from the nearby flight perch. The feeding perch was attached to a balance (P-1040 load cell, Tedea-Huntleigh, Cardiff, UK), and body mass data were automatically stored in a computer at 1 s intervals. Communication with the balances was established using a RS232 serial multiport (C218, Moxa Technologies, Taipei, Taiwan). Pellet dispensers were operated by a PLC (DL205, Koyo, Langerak, The Netherlands) and the activity data were stored in a PC.

The L:D cycle was 14:00 h:10:00 h and food could only be obtained during the light period. For practical reasons the light period was from 00:00 h to 14:00 h, and night started and ended with a 10 min period of dim light. Fresh drinking water was always present, and water for bathing was presented 1 day per week. As a source of complementary nutrients, two mealworms were given three times each week, except during the periods of energy intake measurements. Ambient temperatures were $16.3 \pm 0.1^\circ\text{C}$ (mean \pm S.E.M.) during the night and $17.1 \pm 0^\circ\text{C}$ during the day.

Food pellets (Trouvit Europe Eel, Trouw, France) consisted of proteins (44%), fat (30%) and fibre/ash (20.0%), complemented with vitamins and minerals (manufacturer's specifications). Average fresh mass of one pellet was 0.020 g, with water content 4%. Energy content was 24.7 kJ g^{-1} dry mass; one pellet therefore contained 474 J.

Experimental protocol

The experiment was performed with eight males caught in the wild and housed in an outdoor aviary until the experiment. All birds had prior experience with the system. At the start of the experiment all birds experienced a foraging reward rate of 2.0 return flights per pellet (f/p; the 'rich' environment). After 1 week the foraging reward rate of four birds was gradually decreased to 6.3 f/p over a period of 3 weeks (the 'poor' environment). The other four birds remained in the rich environment. One bird kept losing mass when on a rate of 5.6 f/p, and this bird was therefore kept on a foraging reward rate of 5.0 f/p. The birds stayed on these schedules for a further 2 weeks, and during the last days of this period energy expenditure measurements were taken on all eight birds. Next, the rich and poor feeding conditions were gradually changed to the opposite state. In this transition period all birds remained

on a foraging reward rate of 4.0 f/p ('intermediate' environment) for 1 week to measure their energy budget. Subsequently, foraging reward rates of the birds formerly in the rich condition was steadily decreased over a period of 4 weeks, until one bird was on a rate of 6.3, one at 5.6 and one at 5.0 f/p. The fourth bird died halfway through the experiment from an unidentified disease and was left out from all analyses. The four birds that were initially in the poor environment were gradually brought to a rich, 2.0 f/p regime.

Metabolic measurements

For basal metabolic rate (BMR) measurements the birds were taken from their cages at the end of the light period and kept for the night in an open air flow system for measuring rates of O₂ consumption and CO₂ production. Starlings are post-absorptive after 60–75 min (Karasov, 1990; Levey and Karasov, 1994). During a measurement, a bird was sitting on a perch inside a dark 24 l Plexiglas box at a temperature of 26.5°C, which is within the thermoneutral zone of starlings (Kendeigh et al., 1977; Biebach, 1979, 1984). The air flow rate was controlled by mass-flow controllers (5850S, Brooks, Rijswijk, The Netherlands), that were calibrated with a bubble flow meter (Levy, 1964), set to deliver 40.0 l h⁻¹. In- and out-flowing air was dried by passing through a molecular sieve (3Å, Merck, Darmstadt, Germany). Gas analysis was done using a paramagnetic O₂-analyser (Servomex Xentra 4100, Crowborough, UK) and CO₂-analyser (Servomex 1440). The system was calibrated before each measurement session using two 3-digit precision gas mixtures of 20.0% O₂/0% CO₂ and 21.0% O₂/1.0% CO₂ in N₂. Measurements were recorded at 9 min intervals. The rate of oxygen consumption was calculated from these measurements and converted to the energy equivalent, while correcting for the respiratory quotient, according to Brody (1945). BMR was taken to be the minimum value of a 30 min running mean. Body mass was measured before and after respirometry. Because the temperatures in the flight cages (on average 16.8°C) were within the thermoneutral zone (Kendeigh et al., 1977), respirometer measurements could be applied for night-time energy expenditure (E_{night} , kJ 10 h⁻¹) estimates in the flight cages without temperature corrections.

To estimate the metabolic rate of the starlings during the day when not flying, a separate series of trials was undertaken in which a different group of starlings was kept in smaller cages measuring 40 cm×80 cm×40 cm (height×width×depth), precluding flight activities. Eighteen birds had *ad libitum* food, and an additional six birds were restricted to 70% of the *ad libitum* food intake per day, a reduction similar to the 73% of food eaten by starlings in a poor environment compared to a rich environment. These individual trials lasted approx. 7 days, at the end of which their metabolic rate was monitored for 24 h by respirometry, while maintaining the light:dark schedule.

Daily energy expenditure

DEE was estimated from food consumption, faeces production and mass change. Food consumption was measured

by weighing the food in the pellet dispensers at 48 h intervals. All faeces were collected from the cages, and from the plastic sheets covering the floors for this purpose. Faeces that remained on the sheets after initial cleaning were removed with moist towels of known dry mass. Faeces and towels were weighed after drying for 3 days at 70°C. Energy content of dried food samples and of individual faeces samples were measured using a bomb calorimeter (C5000, IKA, Heitersheim, Germany). DEE was calculated from the metabolisable energy intake (MEI) and body mass changes, according to the equation $DEE = I - E - P$, where I is the gross energy intake, E the energy excreted and P the energy cost of tissue accumulation or energy catabolised from stored tissue, all in kJ day⁻¹. P was estimated to equal mass change × -18.0 kJ g⁻¹ by accurately measuring energy budgets of captive starlings that showed mass changes (S. Verhulst, unpublished data; for method, see Masman, 1986). The assimilation efficiency was calculated as gross energy intake minus energy content of the faeces divided by gross energy intake.

Body mass, pectoral muscle thickness and flight speed

Body mass was measured automatically to the nearest 0.1 g when birds were on their feeding perch, and with an ordinary balance whenever a bird was handled. In this study we used the average mass during the last hour of the active period. Relative pectoral muscle thickness was measured using a 'muscle meter' developed at Max Planck Research Centre for Ornithology (Seewiesen, Germany), which measured, to the nearest 0.1 mm, the distance from the breast surface to a virtual plane perpendicular to the sternum crest, 3.0 mm sideways of the sternum. Three measurements were taken at the location where the sternum protruded furthest from the centre of the body, and the average value was used.

Flight speed was measured early in the morning from video recordings taken from outside the cages through a one-way screen. The time from take-off to landing was measured with a stopwatch for a sample of flights.

Statistics

All mean values are given ± standard error of the mean (S.E.M.). We analysed data with Generalised Linear Models (GLM) and Generalised Linear Mixed Models (GLMM) using SPSS (v. 12.0, SPSS Inc.), except where otherwise stated. We controlled for individual differences by including individual as fixed (GLM) or random (GLMM) effect in the models.

Results

Activity and energy budget

The number of flights and flight time per day increased fourfold with decreasing food availability (see Table 1 for all summary data). Flight speed in the poor environment was 4% lower than in the rich environment, which contributed to the effect of foraging environment on daily flight time. Food intake increased significantly with decreasing food availability, while

Table 1. *Biometrics, activity and energetics in different foraging environments*

	Foraging conditions			Treatment	Time	Order
	Rich	Intermediate	Poor			
Mass and flight muscle						
Body mass (g)	79.8±2.4	72.7±2.1	64.2±1.4	$F_{1,12}=104, P<0.001$	—***	ns
Muscle depression (mm)	2.31±0.24	3.21±0.17	3.39±0.25	$F_{1,12}=18.0, P<0.005$	ns	ns
Activity						
Travel distance (km day ⁻¹)	7.84±0.38	20.38±2.16	31.84±2.74	$F_{1,12}=97.1, P<0.001$	ns	ns
Flight time (min day ⁻¹)	32.2±2.1	85.4±9.3	136.1±12.8	$F_{1,12}=95.8, P<0.001$	ns	ns
Flight speed (m s ⁻¹)	4.08±0.08		3.92±0.09	$F_{1,202}=17.6, P<0.001$	+*	ns
Measured energetics						
Assimilation efficiency	0.826±0.010	0.843±0.014	0.840±0.016	$F_{1,12}=2.76, P=0.12$	+**	ns
MEI (kJ day ⁻¹)	149.8±5.6	189.2±20.3	215.5±9.5	$F_{1,12}=14.4, P<0.005$	ns	ns
DEE (kJ day ⁻¹)	153.8±5.1	192.3±16.2	220.2±10.1	$F_{1,12}=22.9, P<0.001$	ns	ns
E_{night} (kJ day ⁻¹)	37.79±1.01	31.92±1.22	27.54±1.17	$F_{1,12}=65.8, P<0.001$	ns	ns
BMR (W)	0.861±0.019	0.776±0.019	0.692±0.029	$F_{1,12}=53.3, P<0.001$	ns	ns
BMR _{ms} (mW g ⁻¹)	10.85±0.40	10.69±0.27	10.76±0.28	$F_{2,112}=0.03, P=0.88$	ns	+*

Values are means ± S.E.M. (N=7 birds).
MEI, metabolisable energy intake; DEE, daily energy expenditure; E_{night} energy expended; BMR_{ms}, mass-specific BMR.
Flight speed was only measured in the poor and rich environment.
Test statistics are from GLMMs with bird identity as a random effect (see Materials and methods). ‘Time’ is time elapsed since the start of the experiments and ‘order’ is whether the first measurements were in the poor or rich environment (‘+’ indicates higher values in rich environment). ns, $P>0.05$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

assimilation efficiency was independent of foraging environment. Body mass decreased slightly during the measurement periods (-0.22 ± 0.095 g day⁻¹), but the rate of mass loss within measurement periods was independent of food availability ($F_{2,12}=0.06, P=0.95$; using individual slopes within measurement period as dependent variable). Thus birds used on average 3.95 ± 1.72 kJ day⁻¹ from their body stores. Combining data on food consumption, assimilation efficiency and mass change, we found that DEE increased with decreasing food availability; in the poor environment birds spent 43% more energy compared with the rich environment

(Table 1). Time of the treatment, i.e. whether it was the first, second or third measurement series in the experiment, had no effect on DEE (Fig. 4; GLMM: $F_{1,12}=0.01, P=0.9$), nor did the order of treatments (i.e. poor or rich first; $F_{1,5}=2.33, P=0.19$).
BMR decreased by 20% from the rich to the poor environment (Table 1). Within individual birds, BMR was positively related to mass ($F_{1,13}=35.3, P<0.001$) and the slope [logBMR on log(body mass)] was 1.02 ± 0.17 W g⁻¹. Such a steep slope is in agreement with other within-individual studies (see overview in Battley et al., 2001). Metabolic rate decreased over the course of the night and in intermediate and rich conditions reached minimum values after 6–8 h (Fig. 2). In the poor environment, minimum values were reached earlier, after ±4 h. We tested this by comparing the slopes of metabolic rates (MRs) plotted against time for each measurement session; these slopes decreased with decreasing food availability (Fig. 2; $F_{2,12}=17.6, P<0.001$). While BMR decreased by 20% from the rich to the poor environment, E_{night} decreased by 27%. BMR was independent of treatment order (GLMM: $F_{1,5}=0.86, P=0.40$) or time of measurement (GLMM: $F_{1,12}=4.19, P=0.063$), although the latter effect approached significance.
Total nocturnal mass-specific MR decreased with decreasing food availability in the same way as whole-body MR

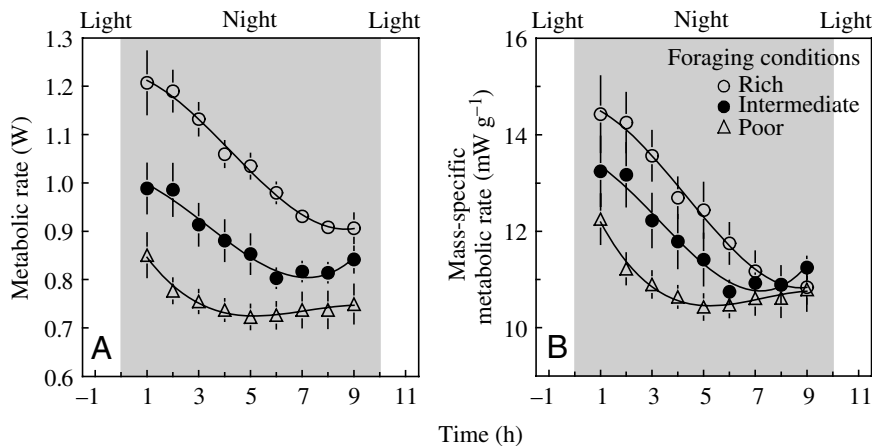


Fig. 2. The hourly averaged metabolic rates (A) and mass-specific metabolic rates (B) for different food availabilities (night from 0 to 10 h, i.e. 14:00 h to 00:00 h local time). Values are means ± S.E.M., N=7. The lines are fitted using 3rd-order polynomials.

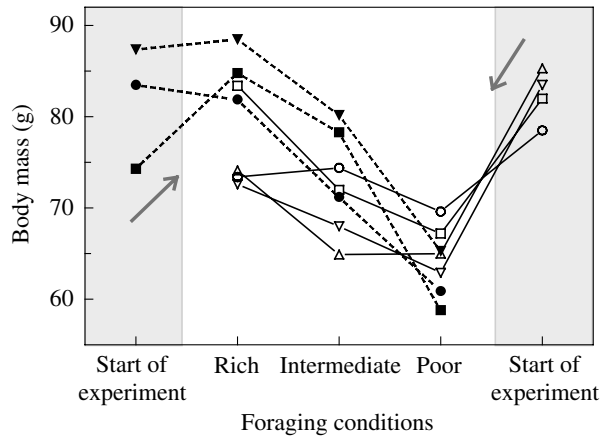


Fig. 3. Body mass in different foraging environments, shown separately for birds that started in the rich environment (closed symbols, broken lines) and poor environment (open symbols, solid lines). Arrows indicate treatment order. Treatment and time had an effect on mass, while order of treatment had not (Table 1).

(Fig. 2). In contrast, mass-specific BMR (BMR_{ms}) was independent of food availability (Table 1).

Body mass and pectoral muscle size

When foraging in the poor environment, birds had 15.6 ± 3.1 g lower body mass as compared to the rich environment, and mass in the intermediate environment was intermediate (Table 1). The range in body mass changes was large, from 3.8 to 26.1 g, and one cause of this variation was the time spent in the cages (Fig. 3): 6.8 ± 1.6 g was lost from the first to the last treatment. Note that initial body mass in the groups starting with different treatments was very similar (Fig. 3).

In the poor environment the pectoral muscle was 1.1 ± 0.2 mm thinner than in the rich environment (Table 1), but between the intermediate and poor environment there was no difference (paired t -test, $t_6 = 0.62$, $P = 0.56$).

Flight costs

Flight costs of starlings were previously estimated, in the same flight cages, at 20.5 ± 0.93 W (Hambly et al., 2004) using labelled bicarbonate (Speakman and Thomson, 1997; Hambly et al., 2002). If flight costs were independent of food availability, the energy allocated to flight would have quadrupled (E_{flight} in Table 2A), due to the fourfold increase in flight time. However, flight costs were measured in the rich environment only, and daily flight costs estimated using instantaneous flight costs of 20.5 W did not fit the energy budget, in particular in the poor environment (given the observed time spent flying and a flight cost of 20.5 W the energy expenditure when not flying would have to be substantially lower than BMR, which is impossible; see below for calculations). We therefore made independent estimates of flight costs for all three experimental treatments using the DEE, activity and respirometer measurements. We estimated how much energy was spent on activities other than flight, and

Table 2. Energy budget calculations based on either (A) fixed flight costs of 20.5 W* and a minimum requirement during the daylight period when not flying ($E = RMR$), or on (B) estimated energy expenditure when not flying during the daylight period

	Foraging conditions		
	Rich	Intermediate	Poor
(A) Flight costs fixed at 20.5 W*			
E_{flight} (kJ day ⁻¹)	39.7±2.6	105.0±11.5	167.4±15.8
$E_{nonflight\ day}$ (kJ day ⁻¹)	51.7±1.1	43.5±1.0	36.2±1.4
$MR_{nonflight\ day}$ (×BMR)	1.84±0.10	1.59±0.19	0.87±0.26
Budget fit (kJ day ⁻¹)	24.6±4.0	11.8±6.4	-10.9±7.5
(B) Flight costs estimated			
$E_{nonflight\ day}$ (kJ day ⁻¹)	82.4±2.2	65.0±2.4	52.2±2.1
E_{flight} (kJ day ⁻¹)	33.6±6.0	95.4±16.9	140.4±9.8
MR_{flight} (W)	16.99±2.37	17.90±1.56	17.50±0.78
Budget fit (kJ day ⁻¹)	0	0	0

RMR, resting metabolic rate (MR); E , energy expenditure.

*Fixed flight costs in A are taken from Hambly et al. (2004).

The calculated energy budget components are within bold borders. Budget fit shows the difference between actual and calculated budgets. Values (mean ± S.E.M.) are averages from calculations for each individual for each treatment.

calculated flight costs under the assumption that the difference between the non-fly budget and the total energy expenditure was spent on flight.

Nocturnal energy expenditure was measured directly (E_{night} , Table 1). For non-flying birds during day-time we multiplied MR_{night} with a scaling factor determined independently using 24 h respirometer measurements on a different group of starlings. These birds stayed at $20.8 \pm 0.2^\circ\text{C}$, were either on *ad libitum* food or food-rationed, had drinking water available and experienced a L:D cycle of 12 h:12 h. We used respirometer boxes that were small enough to constrain activity, and most of the time was spent sitting (P. Wiersma, unpublished observations). From these measurements we calculated MR_{day} and MR_{night} . MR_{day} was correlated with mass ($r = 0.44$, $N = 24$, $P = 0.032$), but more importantly, MR_{day} and MR_{night} were strongly correlated (Fig. 4). We calculated the ratio of MR_{day} to MR_{night} (1.62 ± 0.03), and applied this figure to our current MR_{night} data to predict MR_{day} . Our estimate can be compared with Aschoff and Pohl's allometric relationship for passerines (Aschoff and Pohl, 1970), on the basis that a ratio of 1.42 for RMR_{α}/RMR_{ρ} is predicted. The small difference with our value may be explained by the fact that Aschoff and Pohl used birds permanently in the dark while our birds had light during the day, which is likely to result in higher energy expenditure. Using the estimated MR_{day} in the budget resulted in estimated flight costs of 17.5 ± 0.9 W. Estimates for the rich and intermediate environments did not differ from Hambly et al.'s measured value (one sample $t_{14} < 1.64$, $P > 0.12$; Hambly et al., 2004), but the estimate from the poor environment was significantly lower ($t_{14} = 2.72$, $P = 0.017$). We therefore estimated flight costs in the rich and intermediate environments

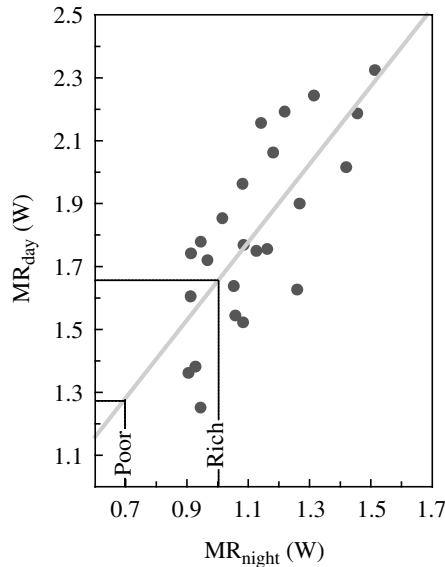


Fig. 4. Association between metabolic rates (measured at $\pm 20.8^{\circ}\text{C}$) of starlings measured during the day (MR_{day}) and the night (MR_{night}) during a 24 h respirometer measurement. MR_{day} and MR_{night} were strongly correlated ($r=0.75$, $N=24$, $P<0.001$, controlling for mass); the regression line is shown. The grey lines show the average values of MR_{night} for our birds and the estimated values of MR_{day} in the rich and poor environment.

at 20.5 W, and consider 17.5 W our best estimate for the poor environment.

Discussion

DEE increased from 154 to 220 kJ day^{-1} from the rich to the poor environment (Fig. 5), and the latter is within the range of brood provisioning starlings, i.e. 200–331 kJ day^{-1} (Westertorp et al., 1982; Ricklefs and Williams, 1984). To our knowledge, this is the first experiment where sustained DEE was elevated by manipulating foraging conditions, providing a potentially valuable new tool to study the physiology of hard work. Note, however, that although DEE increased, we did not observe an accelerated increase in DEE with increasing foraging costs (DEE increased 38.5 kJ from rich to intermediate environment, and 27.9 kJ from intermediate to poor environment). Thus our results only partly match the pattern that we originally predicted (Fig. 1B). This is not surprising, however, since in formulating this prediction we assumed that everything besides foraging costs remained constant, while the starlings demonstrated various energy saving adjustments when food availability decreased.

Our results can be compared with two earlier experiments with starlings foraging in a closed economy. Bautista et al. (1998) used fixed reward rates and found that DEE decreased from 144 kJ to 107 kJ when the environment changed from rich to poor. Fotheringham (1998) used variable reward rates (as did we) and found that DEE was approximately 169 kJ day^{-1} independent of reward rate [estimated by us from

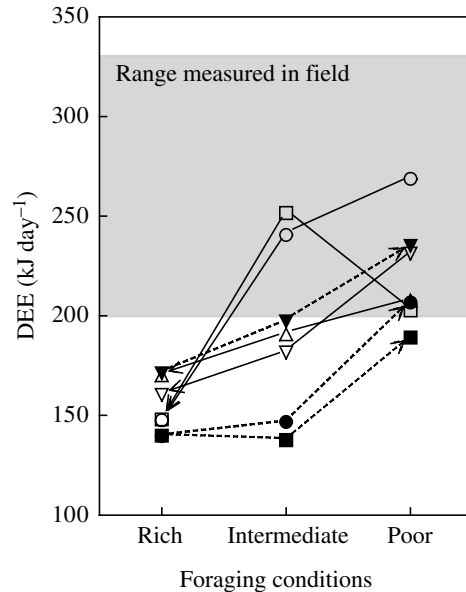


Fig. 5. Daily energy expenditure (DEE) in different foraging environments. The shaded area indicates the range of DEE values measured in brood provisioning starlings in the field (Westertorp et al., 1982; Ricklefs and Williams, 1984). Symbols refer to the same individuals as in Fig. 3, and the arrowheads indicate treatment order.

gross food intake of birds with variable reward rates: approx. 19 g day^{-1} , and energy content and assimilation efficiency from Bautista et al. (1998), who used the same food]. This is comparable to the DEE of our birds in the rich environment (Table 1). The poor environment in our experiment was much harsher than the poorest environment in Fotheringham's experiments: birds in his experiments flew ± 4 km in the poorest environment, which is only 13% of the flight distance in the poor environment in our experiment.

BMR

In the poor environment BMR was 19.6% lower than in the rich environment (Table 1), resulting in an energy saving of 14.6 kJ day^{-1} , in qualitative agreement with comparable studies (Deerenberg et al., 1998; Bautista et al., 1998), and the observed effect of exercise (independent of foraging) in zebra finches (Nudds and Bryant, 2001). The energy savings on BMR were probably for a large part due to mass changes because BMR_{ms} did not differ between foraging environments. This contrasts with the results of lower BMR_{ms} in the poor environment in related studies (Deerenberg et al., 1998; Bautista et al., 1998). That BMR_{ms} was constant is remarkable considering the strong effect of food availability on body mass (-20% in the poor environment). Either body composition did not undergo major changes (which seems unlikely given that the birds became lighter, not smaller), or energy was saved in other ways, e.g. by lowering body temperature (T_b), in which case the constant BMR_{ms} may be coincidence. Hypothermic responses to cope with energy

shortage are common in birds (McKechnie and Lovegrove, 2002), which suggests that this may be a plausible explanation. Savings during the entire night were larger than expected on the basis of BMR alone because metabolic rate decreased more quickly during the night when foraging in the poor environment (Fig. 2). This could also be due to an accelerated decrease of T_b in the course of the night.

Although our finding that BMR was lower in the poor environment is consistent with comparable studies, it contrasts with the notion that BMR is adjusted to work load (Gelineo, 1964; Arieli et al., 1979; Daan et al., 1989; Speakman and McQueenie, 1996; Williams and Tieleman, 2000; Speakman and Selman, 2003). According to this notion we would have predicted BMR to be higher in the poor environment, because of the increase in daytime energy expenditure this induced. Apparently, birds make different physiological adjustments under different ecological circumstances, but it is not evident what triggers these different responses. One could argue that metabolic rate was somehow constrained in the poor environment, forcing the birds to reduce their BMR. However, this is not consistent with the observation that a decrease in BMR was already present in the intermediate environment, while DEE increased further when birds were foraging in the poor environment. Possible constraints on DEE will be discussed below. The experimental protocol followed by our starlings can be looked upon as a training scheme for endurance training, and we see similarities with studies on human exercise physiology. Westerterp (2001) points out that 'novice' trainees for the half-marathon lose body mass and concomitantly lower night-time metabolism. Only professional athletes achieve an increase of BMR at the same mass during training (hinting that a suite of changes are involved). It seems our starlings 'acclimate' to a training programme in much the same way as 'average' human beings do.

Flight costs

We previously estimated starling flight costs in our system at 20.5 W (Hambly et al., 2004; rich environment only). On the basis of this estimate, our birds would have spent 39.7 and 167.4 kJ day⁻¹ on flying in the rich and the poor environment respectively (E_{flight} in Table 2A). However, these estimates are too high to fit the energy budget in the poor environment. Given flight costs of 20.5 W, and the nocturnal energy expenditure as measured, the remaining energy in the poor environment for diurnal metabolic rate when not flying would be $0.87 \times \text{BMR}$, which is clearly impossible (see Table 2A for calculations). Given that total and nocturnal energy expenditure can be measured with reasonable precision, this indicates that flight costs in the poor environment must have been lower than 20.5 W. This would in itself not be surprising, given the low mass in the poor environment, and the effect of mass on flight costs (Pennycuik, 1975; Rayner, 1979; but see Kvist et al., 2001). Note, however, that we could not confirm this directly in our experiment, in the sense that we found no treatment effect on our indirect estimates of flight costs (Table 2A). However, on the basis of an (interspecific) allometric equation of flight costs (Nudds and Bryant, 2000),

one would predict that flight costs should decline by 17% from the rich to the poor environment. This is very close to our budget results (-15%, from 20.5 W to 17.5 W), although we acknowledge that direct measurements of flight costs in different foraging environments will have to be carried out to ascertain lower flight costs in the poor environment.

Effects of time and treatment order

In the course of the experiment the birds lost 6.8 ± 1.6 g body mass (Fig. 3). At the same time flight speed increased slightly by 0.12 ± 0.04 m s⁻¹ (Table 1), which may be due to the lowering of body mass. Treatment had no effect on assimilation efficiency, but there was a small increase over time: 0.037 ± 0.012 from the first to the third measurement (Table 1). Treatment order had no effect on any variable except mass-specific BMR, with birds that started in the rich environment having a 0.99 ± 0.36 mW higher BMR_{ms}. Since the effect was small and statistically weak ($P=0.04$), suggesting it may be a spurious result, we will not further discuss it.

Starving in the midst of plenty?

Compared with free-living birds, mass was exceptionally low when birds foraged in the poor environment (Cramp and Perrins, 1994), suggesting an energy shortage despite the substantial increase in foraging effort and DEE. Energy shortage is also suggested by the accelerated decline in metabolic rate in the course of the night. Given that food availability was in principle unlimited, one could argue that the birds were starving in the midst of plenty. We now examine some hypotheses that could explain why birds did not increase their foraging effort in the poor environment to the level required to maintain the same mass as in the rich environment. To this end we first summarise our findings (Fig. 6) to illustrate the effects of the metabolic adjustments to foraging conditions on the total energy budget. We extended this overview with estimates of the required energy and time budget for the hypothetical case of birds in the poor environment that maintain mass and activity specific metabolic rates as in the rich environment. By lowering mass in the poor environment, and hence maintenance metabolism and probably flight costs, the birds achieved a flight time reduction of 34%, and a 37% reduction in DEE compared with the expected DEE in the absence of such responses (these two percentages differ slightly due to the effect of foraging environment on flight speed; Table 1). Reduced flight costs and maintenance metabolism resulted in approx. 15% reduction in DEE, but the flight time reduction brings about the greatest energy savings, namely approx. 24%. The 27% energy saved during the night gives rise to a further 5% lower DEE.

We now discuss hypotheses that could explain why birds in the poor environment did not maintain body mass as in the rich environment.

Hypothesis 1: time constraints

The length of the working day (14 h) could be insufficient to collect the food required to maintain mass. This seems unlikely

however, because in the poor environment birds still spent only 16.2% of the light period on flying. This increases to 42% of daytime spent on foraging when food handling time is taken into account. Using our energy expenditure measurements (Table 1), we calculated that the flight time should have increased to 25% to maintain mass in the poor environment. Including turning time on the perch and food handling time this would add up to 65% (Fig. 6), which would still leave 35% 'free time'. Since there were no other notable time-consuming activities, we conclude that time was not a limiting factor. Energy expenditure can be constrained by extrinsic or intrinsic constraints (Tinbergen and Verhulst, 2000), but available foraging time seems the only extrinsic constraint present in our system. Since this does not seem an adequate explanation we now turn to intrinsic constraints.

Hypothesis 2: metabolic constraints

It has been suggested that sustained energy expenditure is constrained to approximately $4 \times \text{BMR}$ (Drent and Daan, 1980), and birds spent $3.7 \times \text{BMR}$ in the poor environment, close to this limit. Furthermore, the required DEE to maintain mass in the poor environment (353 kJ; Fig. 6), combined with the BMR in the rich environment, would result in $4.7 \times \text{BMR}$. Although this is high, it is still within the range of values observed (Daan et al., 1990). More importantly, DEE in the poor environment was at the lower end of the range of values reported for free-living starlings feeding nestlings (Fig. 5), suggesting that some increase in DEE was certainly possible. We did not notice symptoms indicating exhaustion, such as difficulties in flying or lethargic behaviour, but cannot rule out that such effects would have occurred when birds had increased their foraging effort to the level required to maintain mass. In conclusion, there was at least some scope for an increase in DEE from an energetic perspective, suggesting that metabolic constraints do not explain why mass was not maintained in the poor environment.

Hypothesis 3: digestive constraints

Digestive bottlenecks can play an important role in foraging decisions (Kersten and Visser, 1996). Starlings have food retention times of 53–59 min, independent of diet (Levey and Karasov, 1994), and we therefore assumed that hourly intake rates over the light period are equal to, or below, maximum sustainable rates. The average food consumption for the different birds was low at $0.56\text{--}0.80 \text{ g h}^{-1}$, well below the maximum hourly consumption rates (range $0.98\text{--}1.4 \text{ g h}^{-1}$). We therefore conclude that DEE was not constrained by a digestive bottleneck.

Hypothesis 4: negative foraging benefits

When flight costs increase with mass, at some mass level the

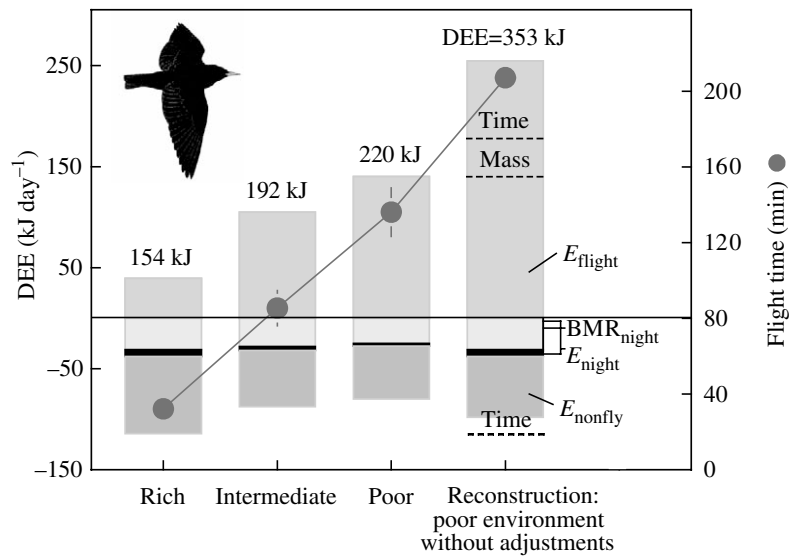


Fig. 6. Energy budgets and flight times in different environments. Also shown (far right) is the hypothetical budget and flight time in the poor environment of starlings that maintain high body mass the same as in the rich environment. E_{flight} is the energy spent on flying, $\text{BMR}_{\text{night}}$ is the energy spent during the night on BMR only, E_{night} is the total energy spent during the night, and $E_{\text{nonfly day}}$ is what is spent during day-time when not flying. The broken lines in the hypothetical energy budget indicate the surplus energy that would have been spent due to the extra time spent flying (and less time spent not flying), and the extra energy that is spent on flying due to the body mass increase. The total daily energy expenditure (DEE) budget is shown on top of each bar.

net energy gain of foraging will become negative, and this could have prevented birds from maintaining high mass in the poor environment. We therefore calculated foraging efficiency and net intake rate in the poor environment for birds with their actual mass and the mass maintained in the rich environment. The effect of body mass (*via* flight and resting metabolism costs) on these foraging currencies was rather small (Table 3). Both currencies became much less attractive when foraging reward rate decreased, but lowering of flight costs through mass loss did not result in substantial improvement. Certainly, no currency would drop to negative values. There is therefore no indication that effects on foraging currencies constrained mass changes.

Hypothesis 5: cognitive processes

Fotheringham (1998) showed that under variable rewards the birds maintained mass and food consumption, but when reward rates were fixed the birds' mass and food consumption decreased when foraging costs increased. We therefore used variable reward rates in our experiments, but cannot exclude the possibility that further modifications in the reward schedule would result in even higher work rates in the poor environment.

Hypothesis 6: ultimate considerations

Given the absence of conspicuous constraints that prevent birds from maintaining a higher mass and energy expenditure in the poor environment, the response to deteriorating foraging

Table 3. Two foraging currencies, net rate and efficiency of energy intake, estimated for different foraging environments and for the hypothetical case of birds with high mass in the poor environment

Environment	Net intake (W)		Efficiency	
	Actual mass	High mass	Actual mass	High mass
Rich	49.8		6.45	
Intermediate	21.2		3.17	
Poor	13.3	12.4	2.52	2.17

Net intake is the difference between the rates of metabolisable energy gain and energy expenditure during a foraging cycle (W). Efficiency is the ratio of metabolisable energy gain over energy expenditure during a foraging cycle (dimensionless). A foraging cycle included the flying time needed to obtain one pellet, the perch time following these flights and the time for handling and eating a pellet (the latter two were estimated at 2 s, but within reasonable limits these estimates had negligible effect). Computations used data from Table 1, and assumed that $MR_{\text{flight}}=20.5$ W in the rich and intermediate environment and $MR_{\text{flight}}=17.5$ W in the poor environment.

conditions can be considered as an optimality problem, i.e. in terms of fitness consequences of different options. Although we cannot estimate the fitness benefits of maintaining high mass, it seems reasonable to assume that if benefits of high mass vary they are likely to be higher in the poor environment, because the probability that food availability drops below a critical level due to stochastic variation is higher when foraging conditions are poor. This suggests that failure to maintain mass in the poor environment is related to fitness costs associated with the high foraging effort this requires (Fig. 6). DEE in the poor environment was slightly lower than in brood-rearing starlings (Fig. 5), but brood-rearing birds accrue fitness benefits from a high DEE (i.e. offspring production), which are absent in our experiments. Absence of such benefits may be part of the explanation why birds were not motivated to further increase their DEE. There is growing evidence that there are trade-offs between work rate and different aspects of somatic maintenance and repair such as immune function (e.g. Sheldon and Verhulst, 1996; Verhulst et al., 2005), and protection against oxidative damage (Wiersma et al., 2004; Alonso-Alvarez et al., 2004). It is therefore plausible that such effects would entail a cost of increasing work rate, but whether such effects really occur in our study system remains to be demonstrated. Nevertheless, given that we consider all other hypotheses less likely, and that trade-offs between work rate and somatic maintenance have been demonstrated in other systems, we consider the costs of increasing work rate the most likely explanation for our finding that birds do not maintain mass in the poor environment.

In conclusion, when trying to understand the effect of food availability on animal behaviour it is important to be aware of the flexibility of the energy budget. For example, energy saving that may be achieved through physiological adjustments may

have significant consequences for individual-based modelling exercises, which explore the relationship between food supply, individual behaviour and population dynamics. Surprisingly, to our best knowledge field data on the relationship between foraging costs per reward and DEE or BMR still have to be collected.

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